Long-term management of *Striga hermonthica*: strategy evaluation with a spatio-temporal population model

T A VAN MOURIK*†, F J J A BIANCHI*‡, W VAN DER WERF* & T J STOMPH*
*Crop and Weed Ecology Group, Wageningen University, Wageningen, the Netherlands, †International Crops Research Institute for the Semi-Arid Tropics, ICRISAT-Bamako, Bamako, Mali, and ‡ CSIRO Entomology, Indooroopilly, Australia

Received 13 April 2007
Revised version accepted 18 February 2008

Summary

The parasitic weed *Striga hermonthica* poses a serious threat to cereal production in sub-Saharan Africa. *Striga hermonthica* seedbanks are long-lived; therefore, long-term effects of control strategies on the seedbank only emerge after several years. We developed a spatially explicit, stochastic model to study the effectiveness of control strategies in preventing invasion of *S. hermonthica* into previously uninfested fields and in reducing established infestations. Spatial expansion of *S. hermonthica* and decrease in millet yield in a field was slower, on average, when stochasticity of attachment of seedlings to the host was included and compared to the deterministic model. The spatial patterns of emerged *S. hermonthica* plants 4–7 years after point inoculation (e.g. seeds in a dung patch) in the spatial-stochastic model resembled the distribution typically observed in farmers' fields. Sensitivity analysis showed that only three out of eight life cycle parameters were of minor importance for seedbank dynamics and millet yield. Weeding and intercropping millet with sesame or cowpea reduced the seedbank in the long term, but rotations of millet with trap crops did not. High seedbank replenishment during years of millet monoculture was not sufficiently offset by seedbank depletion in years of trap crop cultivation. Insight from simulations can be employed in a participatory learning context with farmers to have an impact on *S. hermonthica* control in practice.

Keywords: dispersal, integrated weed management, parasitic weed, weed biology.

VAN MOURIK TA, BIANCHI FJJA, VAN DER WERF W & STOMPH TJ (2008). Long-term management of *Striga hermonthica*: strategy evaluation with a spatio-temporal population model. *Weed Research* **48**, 329–339.

Introduction

Striga hermonthica (Del.) Benth. is a widespread hemiparasitic weed in sub-Saharan Africa, where an estimated 26 million hectares of cereal fields (maize, sorghum and millet) are infested with *S. hermonthica* and *Striga asiatica*, leading to an estimated loss in production of about 10.7 million tons (Gressel *et al.*, 2004). According to farmers in Nigeria, the area and severity of infestation is increasing (Emechebe *et al.*, 2004). New areas and fields are being colonised by the weed by means of cattle dung, infested crop seed and wind (Berner *et al.*, 1994). Despite development of many control strategies and speculations about their long-term effects on the *S. hermonthica* seedbank and cereal yields (Oswald, 2005) there are very few long-term (>3 years) data available.

Integrated weed management requires a long-term approach in addition to prevention of short-term crop losses (Jones & Medd, 2000). The evaluation of effects of control strategies on long-term *S. hermonthica* population dynamics involves long and costly research *programmes*. Modelling weed population dynamics is an attractive approach to assess potential long-term effects of control strategies on the *S. hermonthica* seedbank and cereal yield.

Correspondence: T A Van Mourik, Crop and Weed Ecology Group, Wageningen University, P.O. Box 430, 6700 AK Wageningen, the Netherlands. Tel: (+31) 317483519; Fax: (+31) 317485572; E-mail: tom.vanmourik@icrisatml.org

Five *S. hermonthica* seedbank models have been published (Kunisch *et al.*, 1991; Smith *et al.*, 1993; Smith & Webb, 1996; Mullen *et al.*, 2003; Westerman *et al.*, 2006), but these suffer from three limitations. First, their parameterisation is largely based on fragmented data from a small number of field, pot and laboratory experiments. Second, the models do not incorporate spatial dynamics or stochasticity, which are probably essential components for a realistic description of the colonisation of previously uninfested fields from point inoculations (e.g. a dung patch). Third, except for Mullen *et al.* (2003), earlier models do not link *S. hermonthica* density to cereal yield. The relationship used by Mullen *et al.* (2003) was taken from Webb and Smith (1996) and was originally developed for modelling the competition between non-parasitic weeds and crops (Cousens, 1985). Infection with *S. hermonthica* causes growth reductions in cereals through pathogenic rather than competitive mechanisms. There are few studies on weed population models that include spatial dynamics and stochasticity in the evaluation of management options (Paice *et al.*, 1998; Holst *et al.*, 2007).

In this paper, we use a process-based, spatially explicit and stochastic model to evaluate options for long-term control of *S. hermonthica* infestations in cereal crops. The model is parameterised using empirical data on seed germination and survival, recruitment, survival to maturity, fecundity, seed dispersal and cereal host yield (Berner *et al.*, 1994; Van Mourik, 2007). Six cropping systems (within a single year) and seven rotations of these cropping systems were evaluated to generate plausible projections of long-term *S. hermonthica* dynamics and millet yield.

The objectives of this study were (1) to describe a spatial-stochastic seedbank model for *S. hermonthica*, (2) to study the effects of stochasticity and seed dispersal on the process of colonisation of previously uninfested fields, (3) to study the influence of changes in the life cycle parameters on seedbank dynamics and millet yield and (4) to identify effective control strategies of infested fields in terms of seedbank reduction and millet yield.

Materials and methods

Description of the spatial-stochastic model

The model simulates spread and population dynamics in a stage-structured population of *S. hermonthica* in a cropped field over a sequence of years, with a time step of 1 year. The model was implemented in Matlab 7.0.4 (MathWorks, Massachusetts, USA). We used two spatial scales to model processes that have different spatial resolutions. *Striga hermonthica* population development was described at a coarse spatial scale, whereas seed dispersal was described at a finer spatial scale. On the coarse spatial scale we considered a field (76.8 m × 76.8 m), composed of grid cells that measured 0.8 × 0.8 m. At this coarse scale, each grid cell represents a single host plant (i.e. millet hill), thus in total 96 × 96 hosts were included.

Striga hermonthica seeds are dispersed from mature plants growing on an infected host plant. To describe the spread of seeds we used the finer spatial scale of 0.2 × 0.2 m to keep track of steep gradients in seed densities in between plants. Hence, the area of each plant (0.8 m × 0.8 m) is subdivided in 16 grid cells. At the end of each time step (1 year), dispersed seeds are added to the soil seedbank. Seeds dispersed outside the field area are no longer considered.

We distinguished seven life stages in *S. hermonthica* population development (Fig. 1): viable seeds in the seedbank at the start of the season (S_t), seeds germinated after stimulation by host roots (G), attached seedlings (A), emerged plants (E), mature reproductive plants (R), new seeds produced (P), newly shed viable seeds (V) and viable seeds in the seedbank after the season (S_{t+1}). The population size in each non-seed stage was modelled as a fraction of the population size of the previous life stage (Westerman *et al.*, 2006). Seedbank dynamics from year t to year $t + 1$ was modelled as:

$$S_{t+1} = S_t + V_t - M_t + N_t \quad (1)$$

where S_t and S_{t+1} are the density of viable seeds in the seedbank (seeds/cell) in year t and $t + 1$ respectively, while V_t denotes the density of newly produced, viable seeds (seeds/cell) entering the seedbank in year t, M_t denotes seed removal from the seedbank (seeds/cell) in year t and N_t denotes introduced seeds (seeds/cell). Following the chain of events in the life cycle (Fig. 1), the density of newly produced seeds (V_t) can be expressed as a fraction of the density of viable *S. hermonthica* seeds in the seedbank (S_t):

$$V_t = S_t \cdot g \cdot a \cdot e(A) \cdot r \cdot p \cdot v \quad (2)$$

where g is the proportion of seeds that germinate in response to crop host roots, a is the proportion of germinated seeds that attach to the host root, $e(A)$ is the proportion of attached seedlings that emerge, r is the proportion of emerged plants that reach maturity, p is the seed production per mature plant and v is the proportion of viable seeds (Fig. 1). The attachment of *S. hermonthica* seeds to roots of host plants was modelled as a stochastic process. The density of seedlings that successfully attaches to host plants (A, seeds/cell) was drawn randomly from a Poisson distribution with a mean of μ_A, where μ_A is the product of the density of germinated seeds and the average proportion of

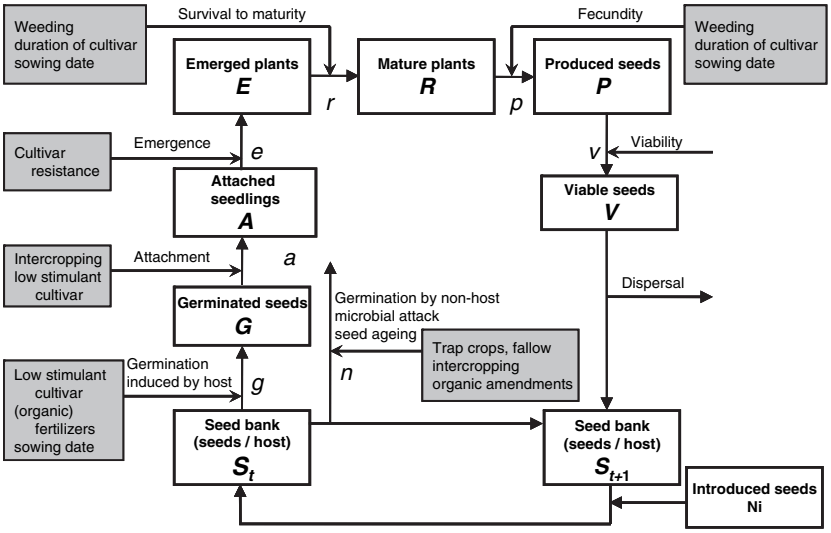

Fig. 1 Diagram of life cycle of *Striga hermonthica*. Model parameters are indicated in italics, white text boxes show state variables and grey text boxes indicate different management strategies that may act on each transition stage.

germinated seeds that attach to the host root (a). The emergence of *S. hermonthica* seedlings on host plants is a density-dependent process. A function was deduced from the model of Yoda *et al.* (1963) for self-thinning of plant populations. We described the proportion of attached seedlings that emerge, $e(A)$, as a function of the density of seedlings that successfully attach to host plants (A):

$$e(A) = \frac{K}{K + A} \tag{3}$$

where K denotes the maximum density of emerged *S. hermonthica* per host plant (Table 1). The number of viable seeds that are lost from a cell (M_t) can be expressed in terms of number of viable seeds in the seedbank (S_t):

$$M_t = S_t \cdot (g + n) \tag{4}$$

where n is the proportion of seeds that die, germinate spontaneously or germinate in response to non-host roots (Table 1).

Mature plants shed seeds that are dispersed and initiate new infestations. We found two distinctive dispersal patterns for *S. hermonthica* seeds: short (at shedding) and long (strong winds) distance dispersal. Both dispersal patterns were described using a Laplace dispersal kernel, essentially a negative exponential function (Skelsey *et al.*, 2005). The spatial profile for dispersal of redistributed seeds is described as:

$$V = m\mathrm{e}^{-q_1 x} + (1 - m)\mathrm{e}^{-q_2 x} \tag{5}$$

where V is the density of viable shed seeds being dispersed to x meters away from the source (maternal plant), m is the proportion of seeds that are dispersed according to the short distance dispersal pattern, and q_1 and q_2 are the slope parameters for short and long distance dispersal respectively (Table 1). Seeds that are redistributed outside the field are lost from the system.

We adjusted a model by Elston *et al.* (1991) that relates yield of potato to the density of root parasitic potato cyst nematodes to model the relationship between the number of *S. hermonthica* seeds (S_t, seeds/cell) and yield of host plants (Y, g/plant):

$$Y = Y_{\max}\left[1 - \frac{(1 - w)S_t}{z + S_t}\right] \tag{6}$$

where $Y_{\max}$ is the expected yield without *S. hermonthica*, w is the minimum yield expressed as fraction of $Y_{\max}$ and z is the density of viable *S. hermonthica* seeds at which half the maximum yield reduction is attained (Table 1).

Parameter estimation

Density-dependent *S. hermonthica* emergence was modelled using the relationship between the density of germinated seeds per host and the recruitment of emerged *S. hermonthica* plants (Van Mourik, 2007). A modified model for self-thinning of populations of plants (Yoda *et al.*, 1963) was fitted using non-linear regression in Genstat 8.0 (VSN International, Hemel Hempstead, UK), assuming a binomial error distribution:

$$E = \frac{a * G}{(1 + c * G)} \tag{7}$$

where E is the number of emerged plants, G is the number of germinated seeds, a is the proportion of successful attachment, and a/c is the maximum number of emerged *S. hermonthica* per host (i.e. K in Eqn. 3) when G approaches infinity (Fig. 2). Goodness-of-fit (RMSE and pseudo R^2) for all fitted equations are given

Table 1 Parameter and SEM values (in parentheses) for six cropping systems: (1) long duration millet; (2) short duration millet; (3) long duration millet with weeding at *S. hermonthica* flowering (~75 DAS); (4) intercrop long duration millet with cowpea; (5) intercrop long duration millet with sesame, and (6) fallow, cowpea or sesame

			Cropping systems											
			Monoculture millet						Intercrop millet-nonhost				Millet absent	
Striga life cycle parameters			Long duration		Short duration		Weeding at flowering		Millet cowpea		Millet sesame		Cowpea, sesame or fallow	
Parameter	Description	Dimensions	1		2		3		4		5		6	
g	Germination in response to host roots	Seed*seed^{-1}	0.6	(0.034)	0.6	(0.034)	0.6	(0.034)	0.3	(0.024)	0.3	(0.024)		
n	Germination through non-hosts + seed death	Seed*seed^{-1}	0.1	(0.409)	0.1	(0.409)	0.1	(0.409)	0.2	(0.037)	0.2	(0.037)	0.4	(0.029)
r	Emerged plants that reach maturity	Plank*planf^{-1}	0.53	(0.018)	0.4	(0.047)	0.02	(0.007)	0.14	(0.056)	0.08	(0.046)	–	
p	Fecundity (seeds per mature plant)	Seed*planf^{-1}	18 800	(1730)	15 600	(2050)	4600	(840)	20 600	(6400)	7200	(1060)	–	
v	Viability of produced seeds	Seed*seed^{-1}	0.8	–	0.8	–	0.8	–	0.8	–	0.8	–	–	
Density-dependent emergence			RMSE = 15.53 R^2 = 0.75		RMSE = 6.52 R^2 = 0.45									
a	Attachment to host roots	Seedling*seed^{-1}	0.0039		0.0101		0.0039		0.00048		0.00012		–	
c	$c = a/K$	–	0.000047		0.000661		0.000047		0.00000580		0.000002		–	
K	Maximum number of *Striga* plants per host	Plant	82.3		16.6		82.3		82.3		82.3		–	
Striga seed dispersal			RMSE = 5.52 R^2 = 0.99											
m	Fraction seed dispersal over short distance	Seed*seed^{-1}	0.88		0.88		0.88		0.88		0.88		–	
q_1	Slope for short distance dispersal	1/m	5.63		5.63		5.63		5.63		5.63		–	
q_2	Slope for long distance dispersal	1/m	0.19		0.19		0.19		0.19		0.19		–	
Millet yield parameters			RMSE = 45.03 R^2 = 0.54		RMSE = 17.10 R^2 = 0.56									
Y_{max}	Maximum millet yield (0 *Striga* seeds)	g*host^{-1}	210		110		210		70		70		0	
w	Minimum millet yield (fraction of maximum) when *Striga* seed density approaches infinity	–	0.0578		0.0712		0.0578		0.0578		0.0578		–	
z	*Striga* seed density at 50% millet damage	g*seed^{-1}	810		340		810		810		810		–	

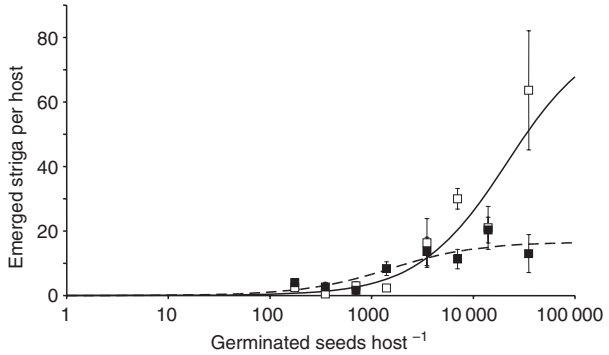

Fig. 2 Measured and fitted relationship between the number of emerged *Striga hermonthica* plants and the number of germinated *S. hermonthica* seeds for a long (□, solid line) and a short (■, dashed line) duration millet cultivar. Vertical bars indicate SEM.

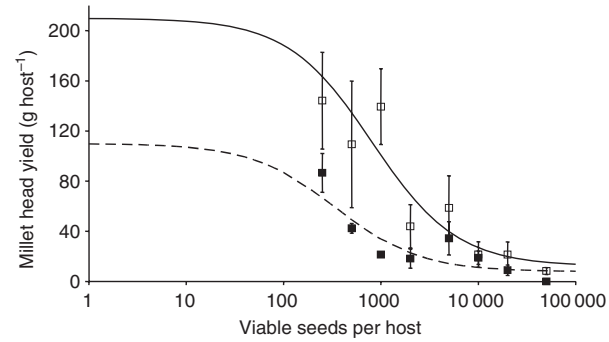

Fig. 3 Measured and fitted relationship between millet head yield and the number of viable *Striga hermonthica* seeds for a long (□, solid line) and a short (■, dashed line) duration millet cultivar. Vertical bars indicate SEM.

in Table 1. The relationship between *S. hermonthica* seed density and millet head yield (Eqn. 6) was fitted using non-linear regression in SlideWrite Plus 6.1 (Advanced Graphics Software, California, USA; Van Mourik, 2007; Fig. 3). Because our data set did not include a control yield in the absence of *S. hermonthica*, the maximum yield was set at an estimated 210 g host^{-1} for a long duration millet cultivar and 110 g host^{-1} for a short duration millet cultivar. The seed dispersal curve (Eqn. 5) was fitted to the relationship between distance from the seed source and seed density in three cereal fields in Nigeria, Benin and West Africa (Berner *et al.*, 1994) using non-linear regression and assuming a Poisson error distribution in Genstat 8 (Table 1). These yields are similar to those of weed-free millet plants in Mali (Webb & Smith, 1996).

Sensitivity analysis

Elasticity of parameters (i.e. the relative change in model output per unit of relative change in the value of a parameter) was calculated as follows:

$$e_\theta = \frac{(Y_{\theta+} - Y_{\theta-})/Y_\theta}{(\theta_+ - \theta_-)/\theta} \quad (8)$$

where e is the local elasticity of a parameter, Y_θ, $Y_{\theta+}$ and $Y_{\theta-}$ are the model outputs (i.e. *S. hermonthica* seedbank density, millet yield or number of infected hosts) at year 3 for the unchanged parameter value θ, a proportionally raised parameter value (θ_+) and a proportionally lowered parameter value (θ_-) after running the model with a point inoculation of 2000 seeds on a central host millet plant in the field using the stochastic model (see Scenarios).

Scenarios

Stochasticity and spatial spread

To study the effect of stochasticity, a spatial-stochastic and a spatial-deterministic model were developed. Furthermore, two inoculation methods were used to study the effect of colonisation of previously uninfested fields. The first inoculation method was a point inoculation of *S. hermonthica* seeds at one host in the centre of the field and the second was a blanket inoculation of all hosts in a field. Simulations with the stochastic model were repeated 200 times and are presented as averages or sometimes as individual realisations.

Cropping systems

The life cycle processes of *S. hermonthica* in six different cropping systems were parameterised using data from field studies (Van Mourik, 2007). These cropping systems were (1) a monoculture of a long duration millet, (2) a monoculture of a short duration millet, (3) a monoculture of a long duration millet with weeding at *S. hermonthica* flowering, (4) an intercrop of a long duration millet with cowpea, (5) an intercrop of a long duration millet with sesame, and (6) a fallow or a trap crop monoculture of cowpea or sesame (Table 1). The following parameters were kept constant for all cropping systems: viability of produced seeds (v), the fraction of dispersed seeds over short distance (m), and the slope for short distance and long distance dispersal (q_1 and q_2 respectively). The parameters for cropping systems 1–6 were used to simulate seedbank dynamics of *S. hermonthica*, the number of hosts infected and host yield over a period of 16 years.

Results

Parameter estimation

The relationship between the number of germinated seeds and the number of emerged plants (Eqn. 3) is presented in Fig. 2. Fits were adequate for the short

duration millet host (R^2 = 0.45 and RMSE = 6.52) and for the local, long duration millet host (R^2 = 0.75 and RMSE = 15.53). The formula used to describe *S. hermonthica* seed dispersal from mature plants (Eqn. 5) gave an excellent fit to the data (R^2 = 0.99 and RMSE = 5.52; Table 1). Finally, the formula for the relationship between millet head yield and *S. hermonthica* seed density (Eqn. 6) gave an acceptable description of the data for the short duration (R^2 = 0.56 and RMSE = 17.10) and the local, long duration millet cultivar (R^2 = 0.54 and RMSE = 45.03; Fig. 3). All fits and parameter estimates are presented in Table 1.

Sensitivity analysis

The elasticity analysis showed that after 3 years of continuous millet cropping (during population increase and expansion phase), five out of the eight parameters were influential in determining seedbank density, millet head yield and the number of infected hosts (Table 2). These were the fraction of seeds that germinate in response to host roots (g), the fraction of germinated seeds that attach to the host root (a), the fraction of emerged plants that reach maturity (r), fecundity (p) and the fraction of seeds that are dispersed over short distance (m). Output variables were less sensitive for changes in the fraction of seeds that germinate in response to non-host roots or die due to other causes (n) or the slope parameters for dispersal over short (q_1) and long distance (q_2).

Scenarios

Stochasticity and spatial spread

In simulations with the stochastic model, establishment of *S. hermonthica* is either a failure or a success.

Table 2 Elasticities for a selection of parameters 3 years after introduction of 2000 seeds in the centre of a field using the spatial-stochastic model

Parameter	Seedbank density	Millet yield	Number hosts infected
g	2.059	*−0.151*	*1.964*
n	−0.126	0.010	−0.112
a	*1.769*	*−0.130*	*1.767*
r	*2.627*	*−0.172*	*1.682*
p	*2.785*	*−0.175*	*1.708*
m	*−2.437*	*0.602*	*−6.240*
q_1	−0.330	0.029	−0.268
q_2	*0.077*	0.050	−0.630

Elasticities have been derived for deviations in parameter values (+10% and −10%) from three output variables (seedbank density, millet head yield and number of infected hosts). The elasticities indicated in italics highlight the most influential parameters. Parameter values and explanation in Table 1.

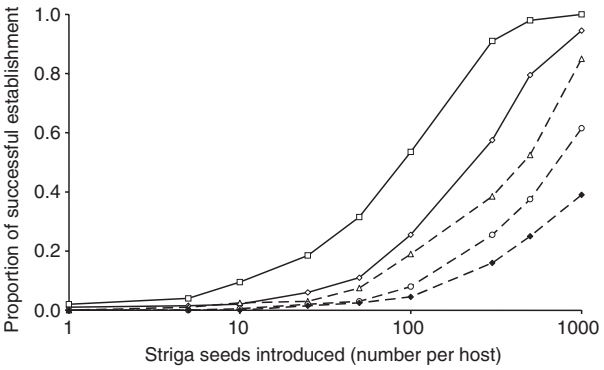

Fig. 4 Simulation of the proportion of successful establishment of *Striga hermonthica* (n = 200) after 12 years of cultivation as a function of the number of *S. hermonthica* seeds introduced to a single host plant in a millet field. Evaluated scenarios are: continuous short duration millet (□), continuous long duration millet (◇), 1 year of non-hosts followed by 3 years long duration millet (Δ), 2 years of non-hosts followed by 2 years long duration millet (○), and 3 years of non-hosts followed by 1 year long duration millet (♦).

Introduction of low densities of *S. hermonthica* seeds to a single host plant in a previously uninfested field mostly resulted in failures, even under a favourable cropping system, but the success rate increased with higher amounts of inoculum (Fig. 4). A point inoculation with a *S. hermonthica* seed density of 1000 per hill resulted in nearly 100% establishment with the short duration millet, but less favourable cropping systems had considerably lower establishment probabilities.

Striga hermonthica seedbank and millet yield dynamics over 12 years after point inoculations of 10 and 1000 seeds differed for the stochastic and deterministic models (Fig. 5). In simulations with the stochastic model, only 2.5% of point inoculations with 10 seeds per hill (5 cases out of 200) resulted in *S. hermonthica* establishment (Fig. 5A). In the few cases that *S. hermonthica* did establish, the initial rise in population level was higher in the stochastic model than in the deterministic model. However, on average the stochastic model led to slower seedbank increase than in the deterministic model and hardly any reduction in millet yield (Fig. 5A, 5B). There is an apparent contradiction between a substantial seedbank increase and a very limited reduction in millet head yield as predicted by the stochastic model. The increase in seedbank density in the five model runs with successful establishment was so huge that, on average, the seedbank increased profoundly, whereas the reduction in yield of these five model runs had only a marginal effect on the average millet head yield of the 200 model runs. After a point inoculation with 1000 seeds, 97.5% of the simulations led to successful *S. hermonthica* establishment in the stochastic model (Fig. 5C). At this density, the average outcome of the stochastic model

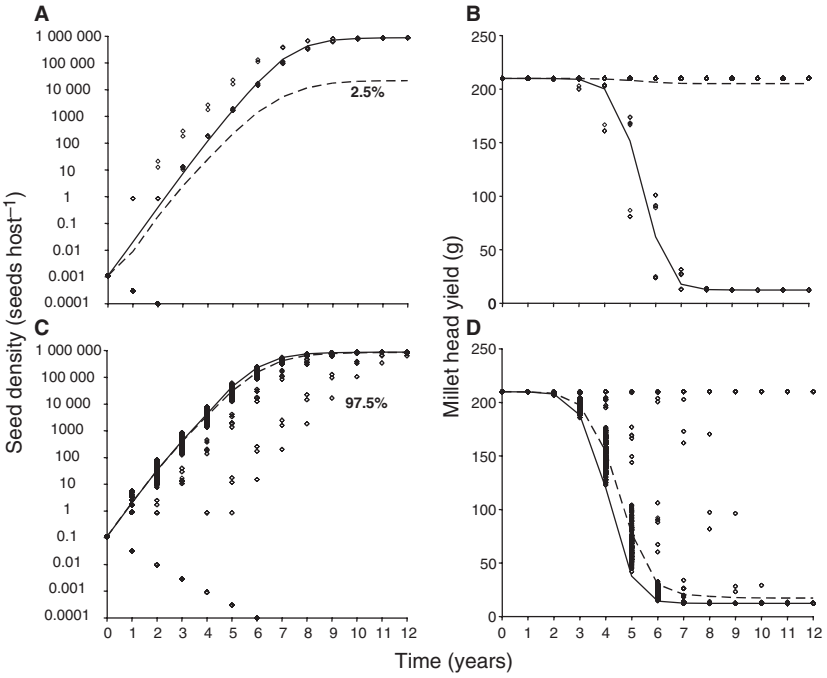

Fig. 5 Simulated seed density of *Striga hermonthica* (A, C) and potential millet head yield (B, D) during 12 years for a monoculture of millet after point inoculation of 10 (A, B) and 1000 (C, D) seeds on a millet host in the centre of the field. The deterministic model is represented by the continuous line. Diamonds indicate individual simulations in the stochastic model and the mean is presented as a dashed line. The percentage successful establishments of *S. hermonthica* are indicated in A and C.

approached that of the deterministic model. In some cases, no establishment from the initial inoculum was observed until 5 years after introduction due to stochastic effects, (Fig. 5C). When using a blanket inoculation, the stochastic and deterministic models yielded nearly similar results, i.e. the effect of stochasticity was largely nullified by the effect of averaging over a population of 96×96 millet plants (data not shown).

The stochastic model generated a highly heterogeneous pattern of *S. hermonthica* infestation around the edges of the dispersal kernel (Fig. 6). At very low densities, *S. hermonthica* plants emerged on just a few hosts and produced a large amount of seeds, most of which stayed close to the centre of dispersal. The following year, this led to spatially heterogeneous emergence patterns. In contrast, the deterministic model generated a homogeneous infestation pattern of *S. hermonthica*. Figure 6 exemplifies a single simulation with the stochastic model in which the rate of spatial expansion from the inoculated spot was larger than that of the deterministic model.

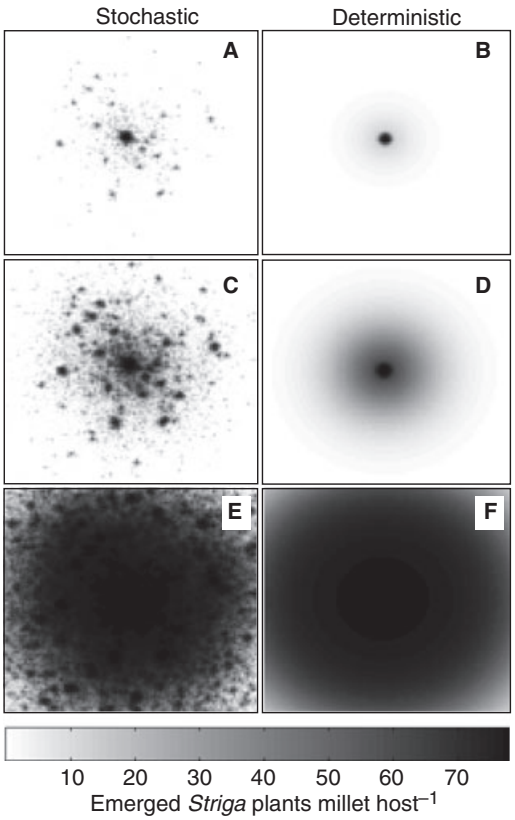

Fig. 6 Simulation of the expansion of a *Striga hermonthica* infestation in a millet field (long duration millet variety) from a single infected host inoculated with 2000 seeds with a model that contains stochasticity (A, C, E) and a deterministic model (B, D, F). Frames A and B, C and D, and E and F depict the number of emerged *S. hermonthica* plants after 4, 5 and 7 years respectively.

Cropping systems

The annual population growth rate (λ) was calculated for cropping systems using the deterministic model and assuming parameter $e(A) = 1$ (Table 3). Cropping systems with $\lambda > 1$ will be considered 'permissive' (scenarios 1 and 2) and those with $\lambda < 1$ 'suppressive' (scenarios 3–6). A monoculture of a long and a short duration millet (scenario 1 and 2) always led to seedbank increase and millet head yield decrease, except when weeding at *S. hermonthica* flowering was performed

Table 3 Evaluated scenarios and their effects on *S. hermonthica* seedbank density, the number of years until 70%, 90% or 98% reduction of the seedbank, the number of infected hosts in year 4, 8 and 12, and cumulative yearly millet head yield in year 4, 8 and 12 (average per host)

			Years until seedbank reduction			% Infected hosts (at year)			Average millet yield ($g_{*}host^{-1}$) (at year)		
Scenario	Cropping system	Seedbank*(λ)	>70%	>90%	>98%	(4)	(8)	(12)	(4)	(8)	(12)
1	Long duration millet	+ (19.0)	–	–	–	100	100	100	37	25	21
2	Short duration millet	+ (30.6)	–	–	–	100	100	100	15	12	10
3	Millet-cowpea intercrop†	– (0.63)	9	12	>15	7.34	3.40	1.56	41	48	52
4	Monoculture non-host	– (0.60)	3	4	7	0	0	0	0	0	0
5	Millet-sesame intercrop†	– (0.30)	3	4	6	0.45	0.04	0	**48**	**58**	**62**
6	Millet with late weeding†	– (0.47)	2	3	6	20.6	1.07	0.05	**149**	**177**	**188**
Rotation of crop systems‡											
7	(4 - 1 - 1 - 1)	+	–	–	–	100	100	100	42	26	20
8	(4 - 4 - 1 - 1)	+	–	–	–	99.7	100	100	48	28	6
9	(4 - 4 - 4 - 1)	+	–	–	–	39.7	73.3	97.6	42	36	29
10	(4 - 3 - 3 - 3)	–	5	9	14	5.50	1.85	0.62	35	46	50
11	(5 - 4 - 3 - 6)	–	3	5	8	38.6	5.36	0.62	**64**	**74**	**78**
12	(4 - 5 - 4 - 3)	–	2	5	8	2.35	0.32	0.05	26	29	31
13	(4 - 5 - 5 - 5)	–	3	4	7	0.51	0.05	0	38	51	52

The stochastic model was used with an initial seedbank density of 1000 seeds per hill (1562.3 seeds m^{-2}). Simulations were repeated 200 times. The population growth rate per year without density-dependent emergence, a spatial component or stochasticity, is denoted as λ.
*+/–; seedbank increase (permissive cropping system)/decrease (suppressive cropping system).
†Intercrops of millet with cowpea or sesame and millet with late weeding (at Striga flowering ~ 75 DAS) were performed with the long duration millet cultivar.
‡Scenarios in cycles of 4 years where 4-1-1-1 means 1 year of a non-host system followed by 3 years of a long duration millet monoculture.

(scenario 6) (Table 3). Rotations of non-hosts (fallow, cowpea or sesame) with millet monoculture for one (scenario 7), two (scenario 8) or three (scenario 9) years in every 4 years still led to a seedbank increase (Table 3, Fig. 7). The low millet head yield in the long term was the result of a high number of infected millet hosts in these systems. Intercropping millet with cowpea (scenario 4) slowly reduced the *S. hermonthica* seedbank and the potential cumulative millet head yield was superior to any of the permissive cropping systems from year 8 onwards (Fig. 7, Table 3).

Among the suppressive scenarios (scenarios 3–6, 10–13), scenario 6 was the most effective strategy in reducing the seedbank and increasing millet head yield after 4, 8 and 12 years (Table 3). An intercrop of millet with sesame (scenario 5) was equally effective as scenario 6 in reducing the *S. hermonthica* seedbank. However, potential millet head yield in scenario 5 was considerably lower than that in scenario 6 due to a lower value of Ymax as a result of competition with sesame (Van Mourik, 2007).

Continuous cropping of cowpea and sesame or a fallow (scenario 4) inevitably leads to a seedbank decrease. However, these strategies were less effective than scenario 5 or 6, because of the low *S. hermonthica* germination rates in non-hosts rotations as compared with intercropping of millet with cowpea or sesame (Tables 1 and 3). Scenario 11 is also interesting as *S. hermonthica* seedbank density decreased quickly in this very diverse system, while the cumulative millet yield is higher than that of continuous millet-sesame

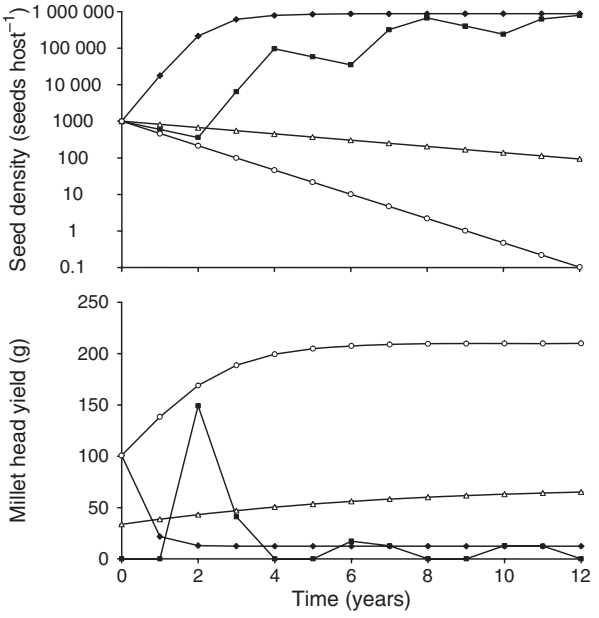

Fig. 7 Simulated seed density of *Striga hermonthica* and millet head yield during 12 years for a monoculture of a long duration millet (♦), a rotation scheme of 2 years of cowpea, sesame or fallow followed by 2 years of a monoculture of a long duration millet (■), a millet-cowpea intercrop (Δ), and millet monoculture with weeding at *S. hermonthica* flowering (○).

intercropping. Furthermore, it is expected that at year 4 of scenario 11, the density of emerged and flowering *S. hermonthica* plants has already decreased considerably, making it less labour intensive than every year weeding in scenario 6.

Discussion

In this paper, a stochastic and spatially explicit model was developed to simulate the population dynamics of *S. hermonthica* and its effects on cereal production systems typically observed in semi-arid sub-Saharan Africa. It is the first model of its kind that includes spatial and stochastic components, enabling an evaluation of effective control strategies to limit the process of colonisation of *S. hermonthica* in previously uninfested fields. Parameters were estimated mostly from new data on life cycle components of *S. hermonthica* on pearl millet under a variety of cropping practices in Niger (Van Mourik, 2007). Simulations indicated that crop rotations with a high proportion of intercrops, and cropping systems that combine cereal monocultures with weeding of *S. hermonthica* will prevent the build up of a seedbank. Cropping sequences that are permissive to *S. hermonthica*, e.g. rotations with a high proportion of cereals and no weeding, will inevitably lead to failure of cereal production. This result was found both with the stochastic and with the deterministic model.

The stochastic model allowed the assessment of the probability of successful establishment in a previously uninfested field, thus creating an opportunity to explore the extent to which cropping systems are vulnerable to invasion. Stochasticity affected seedbank dynamics considerably for point inoculations at low densities, but became less important for blanket inoculations or higher densities point inoculations.

The stochastic model produced very heterogeneous patterns, especially at the fringes of the dispersal kernel where seed densities are very low. These patterns are often observed in fields infested with *S. hermonthica* (Van Delft *et al.*, 1997) and are generally ascribed to soil heterogeneity (Hess *et al.*, 2001). However, these patterns may thus also emerge from the intrinsic behaviour of the seedbank at low densities. Both processes (i.e. stochasticity and soil heterogeneity) likely affect *S. hermonthica* spread and they may interact.

The elasticity analysis indicated that seedbank dynamics was affected by changes in nearly all parameter values of life cycle processes, except for germination in response to non-hosts (n) and the two slope parameters for the dispersal curve (q_1 and q_2). In addition, it appears that the four most sensitive parameters (germination in response to host roots (g), attachment (a), survival to maturity (r) and fecundity (p)) can be manipulated by control strategies, thus efforts should focus on these steps (Fig. 1). The fraction of seeds being dispersed over short distance (m) is probably more difficult to be manipulated by control strategies and so less interesting from a management point of view. Germination and attachment are especially important for the increase in the number of infected millet plants in a field at the increment phase of the seedbank dynamics (i.e. at 3 years after introduction). This has important practical implications, as the *S. hermonthica* seedbank is expected to reach maximum density only rarely, because fields will be abandoned or other crops will be grown, once millet yields start to decrease dramatically.

Validation of the model is problematic because of the lack of long-term field data. However, comparison of model predictions to data from short-term field studies (mentioned below) lends credibility to the model results and inspires trust that the long-term predictions are relevant. For instance, simulations indicate that the most effective control method was a monoculture of millet with weeding at *S. hermonthica* flowering. The effectiveness of hand weeding to restore yields and reduce the *S. hermonthica* seedbank has been demonstrated in pearl millet and maize (Ramaiah, 1987; Ransom & Odhiambo, 1994). The model further suggests that no cropping system or strategy can give satisfactory reduction in seedbank densities (more than 90% reduction) in < 3 years. Indeed, when considering experiments in farmer fields, no experiment has ever shown reductions of more than 90% in seedbank density within 2 to 3 years (Oswald & Ransom, 2001; Abunyewa & Padi, 2003; Murdoch & Kunjo, 2003; Schulz *et al.*, 2003; Franke *et al.*, 2006). This should be taken into account when designing management strategies and discussing options with farmers. The slow reduction of seedbank densities due to germination and seed death, further underscores the need for rigorous prevention of seed production for successful *S. hermonthica* control. This implies that *S. hermonthica* plants escaping control should be killed or removed from a field before they shed seeds. Even if *S. hermonthica* was allowed to produce seeds once every 4 years, a seedbank increase may still be inevitable (Table 3, scenario 9).

Contrary to results from model simulations, many traditional intercropping systems with millet and cowpea often still suffer from high *S. hermonthica* infestations. We suggest two main reasons for this contradiction. First, cowpea is often sown two to four weeks later in the season than millet in farmer practice, whereas in the field experiment used for the parameterisation (Van Mourik, 2007), cowpea was planted at the same time as millet. Second, cowpea sowing density under farmer practice is often very low compared with densities used in the field experiment. Later planting and

lower densities of the cowpea intercrop may compromise the effectiveness of this control option. The option of intercropping as a strategy to control *S. hermonthica* merits further research.

It is likely that the efficacy of control methods as indicated by the model overestimates what can be expected in practice (Van Mourik, 2007). To be effective, different control strategies should be combined in an integrated program to target maximum efficacy for *S. hermonthica* control and cereal yield increase (Debrah, 1994; Oswald, 2005). We do not know how different control strategies interact and whether combinations have additional positive effects in reducing *S. hermonthica* density and increasing crop yields. This is a very important question and should be a priority for future modelling studies and participatory on farm field studies.

Acknowledgements

This research was financially supported by NWO-WOTRO (project W-89-131). We thank Paul Goedhart for statistical advice and Paula Westerman for helpful discussions.

References

Abunyewa AA & Padi FK (2003) Changes in soil fertility and *Striga hermonthica* prevalence associated with legume and cereal cultivation in the Sudan savannah zone of Ghana. *Land Degradation & Development* **14,** 335–343.

Berner DK, Cardwell KF, Faturoti BO, Ikie FO & Williams OA (1994) Relative roles of wind, crop seeds, and cattle in dispersal of *Striga* spp. *Plant Disease* **78,** 402–406.

Cousens R (1985) An empirical model relating crop yield to weed and crop density and a statistical comparison with other models. *Journal of Agricultural Science* **105,** 513–521.

Debrah SK (1994) Socio-economic constraints to the adoption of weed control techniques: the case of *Striga* control in the West African semi-arid tropics. *International Journal of Pest Management* **40,** 153–158.

Elston DA, Philips MS & Trudgill DL (1991) The relationship between initial population density of potato cyst nematode *Globodera pallida* and the yield of partially resistant potatoes. *Revue de Nématologie* **14,** 213–219.

Emechebe AM, Ellis-Jones J, Schulz S *et al.* (2004) Farmers' perception of the Striga problem and its control in northern Nigeria. *Experimental Agriculture* **40,** 215–232.

Franke AC, Ellis-Jones J, Tarawali G *et al.* (2006) Evaluating and scaling-up integrated *Striga hermonthica* control technologies among farmers in northern Nigeria. *Crop Protection* **25,** 868–878.

Gressel J, Hanafi A, Head G *et al.* (2004) Major heretofore intractable biotic constraints to African food security that may be amenable to novel biotechnological solutions. *Crop Protection* **23,** 661–689.

Hess D, Van Lieshout MC, Payne B & Stein A (2001) A review of spatio-temporal modelling of quadrat count data with application to Striga occurrence in a pearl millet field. *International Journal of Applied Earth Observation and Geoinformation* **2,** 133–138.

Holst N, Rasmussen IA & Bastiaans L (2007) Field weed population dynamics: a review of model approaches and applications. *Weed Research* **47,** 1–14.

Jones RE & Medd RW (2000) Economic thresholds and the case for longer term approaches to population management of weeds. *Weed Technology* **14,** 337–350.

Kunisch M, Linke HH, Richter O & Koch W (1991) Inclusion of conceptual modeling in studies on the population dynamics of the genus *Striga*. *Angwandte Botanik* **65,** 45–57.

Mullen JD, Taylor DB, Fofana M & Kebe D (2003) A bio-economic model of long-run *Striga* control with an application to subsistence farming in Mali. *International Journal of Pest Management* **49,** 251–264.

Murdoch AJ & Kunjo EM (2003) Depletion of natural soil seedbanks of *Striga hermonthica* in West Africa under different integrated management regimes. *Aspects of Applied Biology* **69,** 261–268.

Oswald A (2005) *Striga* control-technologies and their dissemination. *Crop Protection* **24,** 333–342.

Oswald A & Ransom JK (2001) *Striga* control and improved farm productivity using crop rotation. *Crop Protection* **20,** 113–120.

Paice MER, Day W, Rew LJ & Howard A (1998) A stochastic simulation model for evaluating the concept of patch spraying. *Weed Research* **38,** 373–388.

Ramaiah KV (1987) Control of *Striga* and *Orobanche* species – a review. In: *Proceedings 1987 The 4th International Symposium on Parasitic Flowering Plants, Marburg, Germany* (eds HC Weber & W Forstreuter), 637–664. Philipps Universität, Marburg, Germany.

Ransom JK & Odhiambo GD (1994) Long-term effects of fertility and hand weeding on Striga in maize. In: *Biology and Management of Orobanche and Related Striga* Research (eds AH Pieterse, JAC Verkleij & JS Ter Borgh), 513–519. Royal Tropical Institute, Amsterdam, the Netherlands.

Schulz S, Hussaini MA, Kling JG, Berner DK & Ikie FO (2003) Evaluation of integrated *Striga hermonthica* control technologies under farmer management. *Experimental Agriculture* **39,** 99–108.

Skelsey P, Rossing WAH, Kessel GJT, Powell J & Van Der Werf W (2005) Influence of host diversity on development of epidemics: an evaluation and elaboration of mixture theory. *Phytopathology* **95,** 328–338.

Smith MC & Webb M (1996) Estimation of the seedbank of *Striga* spp. (Scrophulariaceae) in Malian fields and the implications for a model of biocontrol of Striga hermonthica. *Weed Research* **36,** 85–92.

Smith MC, Holt J & Webb M (1993) Population model of the parasitic weed *Striga hermonthica* (Scrophulariaceae) to investigate the potential of *Smicronyx umbrinus* (Coleoptera: Curculionidae) for biological control in Mali. *Crop Protection* **12,** 470–476.

Van Delft GJ, Graves JD, Fitter A & Pruiksma MA (1997) Spatial distribution and population dynamics of *Striga*

hermonthica seeds in naturally infested farm soils. *Plant and Soil* **195,** 1–15.

Van Mourik TA (2007) *Striga hermonthica* Seed Bank Dynamics: Process Quantification and Modelling. PhD thesis, Wageningen University, Wageningen, the Netherlands.

Webb M & Smith MC (1996) Biology of *Striga hermonthica* (Scrophulariaceae) in Sahelian Mali: effects on pearl millet yield and prospects of control. *Weed Research* **36,** 203–211.

Westerman PR, Van Ast A, Stomph TJ & Van Der Werf W (2006) Long-term management of the parasitic weed *Striga hermonthica*: strategy evaluation with a population model. *Crop Protection* **26,** 219–227.

Yoda K, Kira T, Ogawa H & Hozumi K (1963) Self-thinning in over-crowded pure stands under cultivated and natural conditions. *Journal of Biology* **14,** 107–129.

